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IS MELANIN A DEFENSE AGAINST FEATHER-FEEDING LICE?

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Abstract.—The adaptive basis of plumage color has received much attention, including the finding that color can reveal information about parasite loads to potential mates. A related possibility, that color may be a direct defense against parasites, has received less attention. Melanin makes feathers tough and more resistant to wear and tear. Melanin may also make feathers more difficult for feather-feeding parasites to eat. We explored the role of melanin as a possible ectoparasite defense using Rock Pigeons (*Columba livia*) and their feather-feeding lice (Insecta: Phthiraptera). Rock Pigeons are an ideal species for such work because of the extreme variation in the feathers of different color morphs, ranging from melanin-rich black to melanin-free white individuals. We tested the effect of melanin on lice in several ways. First, we compared the natural louse loads of free-ranging pigeons to see whether the more melanistic color morphs had fewer lice. We also did laboratory assays in which we measured the survival and reproductive success of pigeon lice forced to feed on feathers with different amounts of melanin, and we compared the quantities of feather material consumed by these lice. Finally, we tested the habitat and feeding preferences of lice exposed to feathers with different amounts of melanin. None of our tests revealed any effect of melanin on lice. We conclude that melanin is not, at least in Rock Pigeons, a defense against feather lice.
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¿Es la Melanina una Defensa Contra los Piojos que se Alimentan de Plumas?

Resumen.—La base adaptativa del color del plumaje ha recibido mucha atención, incluyendo el descubrimiento de que el color puede revelar información sobre la carga parasitaria de las potenciales parejas. La posibilidad de que el color pueda ser una defensa directa contra los parásitos ha recibido menos atención. La melanina hace que las plumas sean duras y más resistentes al uso y a desgarrarse y también puede hacer que las plumas sean más difíciles de comer para los parásitos que se alimentan de ellas. Exploramos el rol de la melanina como una posible defensa contra los ectoparásitos usando a *Columba livia* y a los piojos que se alimentan de sus plumas (Insecta: Phthiraptera). *C. livia* es una especie ideal para este trabajo debido a la variación extrema del color de las plumas de las distintas formas, que van desde individuos negros ricos en melanina hasta individuos blancos libres de melanina. Evaluamos el efecto de la melanina sobre los piojos de distintas maneras. Primero, comparamos las cargas naturales de piojos de palomas libres para ver si las formas con más melanina tenían menos piojos. También realizamos ensayos de laboratorio en donde medimos la supervivencia y el éxito reproductivo de piojos forzados a

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alimentarse de plumas con diferentes cantidades de melanina y comparamos las cantidades de material de las plumas consumidas por estos piojos. Finalmente, evaluamos las preferencias de hábitat y alimenticias de los piojos expuestos a plumas con diferentes cantidades de melanina. Ninguna de nuestras pruebas reveló un efecto de la melanina sobre los piojos. Concluimos que la melanina no es una defensa contra los piojos de las plumas, al menos en *C. livia*.

AVIAN PLUMAGE COLORATION is caused by the physical structure of feathers or by pigments in feathers (Gill 1995). Plumage coloration has many functions, including camouflage, thermoregulation, and conspecific signaling (Savalli 1995). The role of coloration in sexual selection has received a great deal of attention in recent years, including tests of the hypothesis that color may be an honest signal revealing information concerning parasite loads (Jawor and Breitwisch 2003). For example, Fitze and Richner (2002) showed that flea-infested Great Tits (*Parus major*) have smaller melanin-based breast stripes than birds without fleas. This fact may allow Great Tits to evaluate the resistance of potential mates by scrutinizing the size of the breast stripe. Melanin may also be a direct defense against parasites, though this hypothesis has received little attention. Melanin has been shown to increase resistance to abrasion (Burtt 1979, 1986; Barrowclough and Sibley 1980), and feather hardness (Bonser 1995). These properties may explain why feather-degrading bacteria are less able to degrade melanin-rich feathers (Goldstein et al. 2004). Here, we explore the possibility that melanin may also deter arthropod ectoparasites, such as feather-feeding lice, which use their mandibles to slice through feather barbules.

Kose et al. (1999) reported that lice (*Hirundoecus malleus*) from Barn Swallows (*Hirundo rustica*) spend significantly more time on white than on black portions of host tail-feathers in petri dishes. Holes chewed by these lice (Møller 1991) are also more abundant on white than on black regions of the tails of wild Barn Swallows. These results are consistent with the hypothesis that melanin deters feather lice, though a direct test of the possible effect of melanin on lice has not been previously been done. We tested melanin as a defense against ectoparasites in a model system consisting of Rock Pigeons (*Columba livia*) and feather-feeding lice.

Rock Pigeons, native to the Old World, were introduced to the New World in the form of escaped domestic pigeons ~400 years ago (Schorger 1952). The extreme color variation of Rock Pigeons, which resulted from artificial selection of domestic stock, makes them an ideal species in which to study the potential effect of melanin on ectoparasites. Feral Rock Pigeons have several color morphs (Johnston and Janiga 1995), including: (1) wild-type "blue-bar" birds, which are bluish gray overall, with dark wing bars; (2) "blue-checker" birds, in which the wing bars have fractured into a checker pattern on the wings; (3) "blue-T" birds, which have a very dense checker pattern; (4) "spread" birds, which are virtually black; (5) "white" birds, which have little or no melanin; and (6) "ash" birds, which have a reddish hue (Haase et al. 1992).

Like mammals and other birds, Rock Pigeons have two types of melanin: eumelanin and phaeomelanin (Durrer 1986). The blue-gray and black colors of wild-type pigeons are predominantly caused by eumelanin. When examined under the microscope, blue-gray feathers resemble a half-tone print, with each barbule having striations or clumping of black melanin granules (Haase et al. 1992). Black regions of the plumage have little striation or clumping. Instead, the granules spread and coalesce, which is why black color morphs are called "spread." The reddish hue of ash birds is predominantly caused by phaeomelanin, not by carotenoids as one might think. Thus, melanin underlies a variety of colors in Rock Pigeons, ranging from black to blue to red (Haase et al. 1992).

Rock Pigeons support two common species of host-specific feather-feeding lice (Phthiraptera: Ischnocera), commonly known as "wing lice" (*Columbicola columbae*) and "body lice" (*Campanulotes compar*) (Clayton et al. 1999). Wing lice spend most of their time on the wings (and tail) and lay their eggs there. Body lice spend most of their time and lay their eggs on the host's abdomen (Nelson and Murray 1971). Both species are permanent parasites that complete their entire life cycle on the

host's feathers and are transmitted to new hosts mainly during periods of direct contact between host individuals (Clayton and Tompkins 1994). Despite spending time on different regions of the host's body, wing and body lice feed on the same type of feathers: the downy portions of abdominal contour feathers.

We used Rock Pigeons to test the potential effect of melanin on lice in several ways. First, we compared the natural louse loads of free-ranging pigeons to see whether more-melanistic color morphs have fewer lice. We also conducted laboratory assays in which we measured the survival and reproductive success of pigeon lice forced to feed on feathers of different colors, and we compared the amount of feather material consumed by these lice. Finally, we tested the habitat and feeding preferences of lice exposed to feathers of different colors.

Methods

Parasite Loads of Free-ranging Birds

We tested for a relationship between color and parasite load by comparing the abundance of lice on free-ranging Rock Pigeons of five color morphs: blue-bar, blue-checker, blue-T, spread, and ash (white birds were rare at our field site). We controlled for regional and temporal variation in parasite loads by capturing 88 birds within an 80-km radius of Kankakee, Illinois, during a single week (6–13 July 1999). Birds were captured using mist nets and single-cell walk-in traps set beneath bridges over roads and streams. Upon capture, birds were immediately sacrificed, placed individually in Ziploc bags, and frozen. Their louse loads were later quantified in the lab using the "body washing" method of Clayton and Drown (2001), which accounts for ~99% of the lice on individual birds. The number of lice on each bird was determined using $y = (1.10[x^{1/2}])^2$ for wing lice, and $y = (1.05[x^{1/2}])^2$ for body lice, where x is the number of lice recovered by washing. These equations were derived from re-analysis of washing data in Clayton and Drown (2001), but with the regressions forced through the origin ($r^2 = 0.99$; $P < 0.0001$ for both wing and body lice) to make the estimates for wing and body lice comparable. Prior to analyses, louse load data were normalized using *ln* transformations.

Experiment I: Parasite Survival and Feeding Rates

In experiment I, we tested the ability of wing and body lice to feed and survive on feathers from four color morphs representing the full melanin spectrum: white (no melanin), blue-bar (moderate eumelanin), spread (predominantly eumelanin), and ash (predominantly phaeomelanin). We captured and sacrificed 15 individuals of each morph in Salt Lake City, Utah, using walk-in traps. We plucked 15 abdominal contour feathers from each bird and stored them in a freezer (4°C). At the start of the experiment, feathers were placed in 50-mL glass tubes lined with paper. The 15 feathers from each individual bird were randomly divided into three tubes with 5 feathers per tube. This was repeated for every bird (15 per color morph), so that each color treatment had a total of 45 tubes. Tubes were placed in a Percival incubator (Percival Scientific, Perry, Iowa) and kept at 33°C and 75% relative humidity on a 12-h light–dark photoperiod (Clayton et al. 2003). We waited 24 h for feathers to absorb moisture in the humid incubator, then removed the feathers from each tube and weighed them to the nearest 0.1 mg three separate times on an analytical balance. Feathers were then returned to the tubes. Initial feather mass per tube was taken as the mean of the three weighings.

After returning the feathers to the tubes, we randomly added 10 adult wing lice to each of 15 tubes per color morph. Ten adult body lice were randomly added to each of another 15 tubes per color morph. The remaining tubes (15 per morph) served as louse-free controls to monitor any background changes in feather mass. Lice were obtained from culture stocks bred on recently captured Rock Pigeons; culture stocks were direct descendents of natural louse populations. The 180 tubes were returned to the incubator for the duration of the two-week experiment.

At the end of the experiment, we tallied the number of live lice remaining in each tube. We also calculated the feeding rates of lice in each tube by again weighing the feathers three times (after removing the lice). We compared the mean feather mass of each tube at the end of the experiment to the initial feather mass for that tube at the start of the experiment. We also collected louse frass (feces) from the bottom of

each tube to make qualitative observations of frass color.

Experiment II: Parasite Reproduction, Habitat Preference, and Feeding Preference

In experiment II, we compared the survival and reproductive rates of lice on the two most extreme color morphs (white and spread) and tested for habitat and feeding preferences of lice exposed to white and spread feathers simultaneously. This experiment was restricted to wing lice, because body lice will not reproduce in our incubator. We ran the experiment for four weeks, which exceeds the 21-day generation time of wing lice (Martin 1934).

As before, we plucked 15 abdominal contour feathers from each of 15 white and 15 spread birds, for a total of 225 feathers per color morph. Feathers were stored in a freezer at 4°C. At the start of the experiment, we placed feathers in 50-mL tubes lined with paper. Because this experiment ran twice as long as experiment I, we used twice as many feathers (n = 10) per tube, with a total of 15 "white" tubes, 15 "spread" tubes, and another 15 "mixed" tubes with 5 white and 5 spread feathers each. After 24 h in the incubator, initial feather mass was calculated as in experiment I. White and spread feathers from mixed tubes were weighed separately to compare relative feather consumption.

After returning the feathers to the tubes, we randomly added 10 adult wing lice to each of the 45 tubes, which were then returned to the incubator. Tubes were removed from the incubator at weekly intervals to census the number of adult and immature lice in each tube, and to note the number of lice on white compared with spread feathers in each of the mixed tubes.

At the end of the four-week experiment, all lice were removed from the tubes, and the feathers in each tube were weighed three times to calculate mean final feather mass, as in experiment I. The final masses of white and spread feathers in the mixed tubes were calculated separately. As a measure of feeding rate, we compared the mean feather mass from each tube at the end of the experiment with the initial feather mass for that tube at the start of the experiment. We calculated the rate of feeding on white and spread feathers from mixed tubes separately. We again collected louse frass from the bottom of each tube for qualitative observations of its color.

Statistical Analyses

Data were analyzed using STATVIEW (Abacus Concepts, Berkeley, California) and G*POWER (Buchner et al. 1997) with an error rate set at 0.1 (Wright 1992, Kose et al. 1999). Effect size (ES) was set at $ES_f = 0.4$ (analysis of variance [ANOVA]) or $ES_d = 0.8$ (t-test) (Cohen 1988, Thomas 1997), which is consistent with the effects of other avian defenses against lice (Clayton and Vernon 1993, Moyer and Wagenbach 1995, Dumbacher 1999).

Results

Parasite Loads of Free-ranging Birds

We trapped the following numbers of birds of each of the five color morphs: 16 blue-bar, 18 blue-checker, 39 blue-T, 5 ash, and 10 spread. We first analyzed the relationship of plumage color to louse load separately for the two species of lice. The abundance of wing lice differed significantly among the five color morphs (one-way ANOVA: F = 2.75, df = 4 and 83, P = 0.03). Specifically, ash pigeons had significantly fewer wing lice than blue-checker or spread pigeons (Fig. 1). By contrast, the abundance of body lice did not differ significantly among the morphs (F = 0.21, df = 4 and 83, P = 0.93, power = 0.91; Fig. 1). When the two species of lice were analyzed simultaneously, however, louse load did not differ significantly among the color morphs (multiple analysis of variance [MANOVA], Wilks' lambda: F = 1.61, df = 8 and 164, P = 0.13, power = 0.99).

Experiment I

Survival.—There was a significant difference in survival between the two louse species (Table 1 and Fig. 2A). More wing lice than body lice survived the two-week period in the incubator; mean number of wing lice was 7.0 ± 0.2, compared with a mean of 4.0 ± 0.3 body lice (all means are presented ± SE). However, there was no significant difference in the survival of either species of louse among the host-color treatments (Table 1 and Fig. 2A).

Feeding rates.—Feathers in louse-free control tubes showed a slight increase in mass (mean = 1.2%) by the end of the two-week experiment. The increase, presumably attributable to water

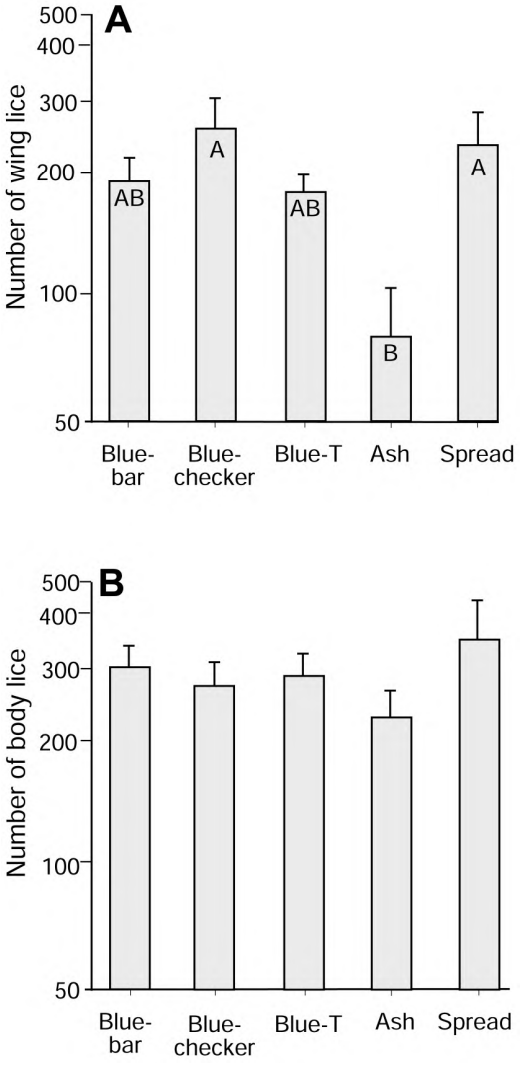

FIG. 1. Mean (+SE) number of (A) wing lice and (B) body lice on five color morphs of free-ranging Rock Pigeons from northern Illinois. Blue-bar and blue-checker birds have similar amounts of eumelanin, but in different patterns; blue-T birds have more eumelanin, and spread birds have the most eumelanin. Ash birds have mostly phaeomelanin, giving them a reddish hue (see text for further details). Sample sizes are as follows: blue-bar, $n = 16$; blue-checker, $n = 18$; blue-T, $n = 39$; ash, $n = 5$; spread, $n = 10$. Note natural log scale on y-axes. Bars with different upper-case letters differ significantly (Tukey-Kramer *post-hoc* tests: ash vs. blue-checker, $P = 0.021$; ash vs. spread, $P = 0.042$).

absorption in the humid incubator, did not differ significantly among the color morphs: white = 0.4 ± 0.2 mg; blue-bar = 0.8 ± 0.3 mg; spread = 0.4 ± 0.2 mg; ash = 0.7 ± 0.3 mg (one-way ANOVA: $F = 0.76$, df = 3 and 56, $P = 0.52$, power = 0.81).

Tubes with lice showed a reduction in feather mass by the end of the experiment. Feathers in tubes with wing lice decreased an average of 7.2% (–3.5 ± 0.2 mg), whereas those in tubes with body lice decreased an average of 5.4% (–2.6 ± 0.1 mg); tubes with wing lice lost significantly more feather mass than tubes with body lice (Table 1 and Fig. 2B). However, the reduction in feather mass did not differ significantly among host-color treatments for wing lice or body lice (Table 1). Frass accumulated at the base of the glass tubes, which shows that the reduction in feather mass is attributable to the consumption of feathers by lice. The color of the frass was similar to the color of the feathers in each tube.

EXPERIMENT II

Survival and reproduction.—Lice in all three host-color treatments survived and reproduced over the course of the four-week experiment (Fig. 3). Adult louse mortality averaged 30–40% (Fig. 3), which is expected given the limited (4–7 week) adult life span of *C. columbae* (Martin 1934). Two immature lice, on average, were present in each tube at the end of the experiment (Fig. 3); this is a fairly typical reproductive rate for *C. columbae* breeding *in vitro* (S. E. Bush et al. unpubl. data). Over the course of the weekly censuses, the number of lice did not differ significantly among the three host-color treatments (repeated-measures ANOVA, effect of treatment: $F = 1.03$, df = 2 and 168, $P = 0.37$, power = 1.0), nor was there a significant treatment * time interaction ($F = 0.59$, df = 8 and 168, $P = 0.78$, power = 0.99).

Habitat preference and feeding preference.—Lice in mixed tubes showed no significant habitat preference. Over the course of the weekly censuses, a mean of 8.2 ± 1.46 lice was observed on white feathers, compared with a mean of 7.9 ± 1.37 lice on spread feathers (paired t-test: $t = 0.17$, df = 14, $P = 0.87$, power = 0.69). Mass of feathers in all tubes decreased an average of 6.7% by the end of the experiment. This decrease in feather mass in experiment II was

TABLE 1. Two-way ANOVAs testing the effects of host color morph and louse species (wing lice vs. body lice) on louse survival and feeding rates in experiment I. Statistical power was 0.98 for both ANOVAs.

	df	*F* ratio	*P*
Louse survival			
Host color morph	3 and 112	1.81	0.1488
Louse species	1 and 112	91.76	<0.0001
Host color morph * louse species	3 and 112	0.51	0.6739
Louse feeding rate			
Host color morph	3 and 112	1.00	0.3979
Louse species	1 and 112	16.42	<0.0001
Host color morph * louse species	3 and 112	0.52	0.6685

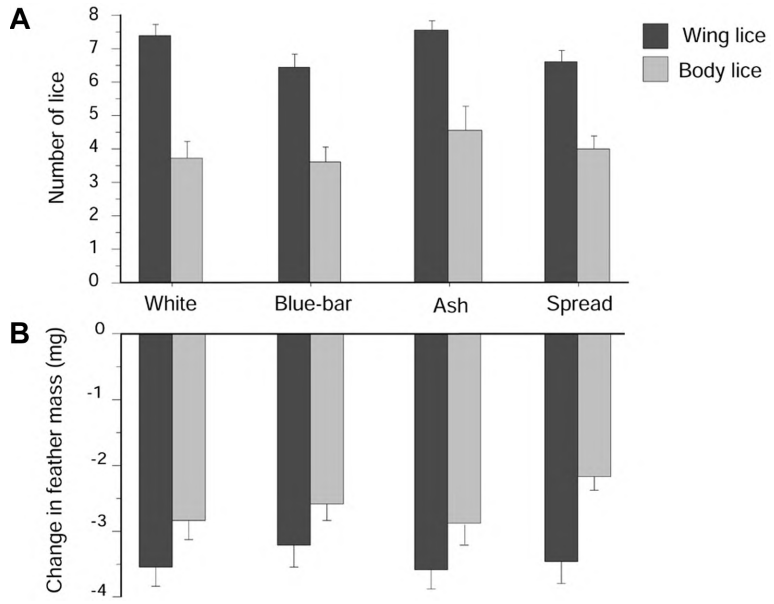

FIG. 2. Experiment I: Survival (A) and feeding rates (B) of wing lice and body lice in tubes containing feathers of different colors (n = 15 tubes per treatment): (A) mean (±SE) number of lice alive after two weeks; (B) mean (±SE) reduction in feather mass after two weeks.

similar in magnitude to the decrease observed in experiment I (experiment II started with twice as many feathers but ran twice as long). The lice showed no significant feeding preferences; the reduction in feather mass did not differ significantly among the three treatments (one-way ANOVA: F = 0.09, df = 2 and 42, P = 0.91, power = 0.75; Fig. 4). Furthermore, lice in the mixed tubes consumed a mean of 3.9 ± 0.5 mg of white feathers, compared with 3.5 ± 0.6 mg of spread feathers, which was not a significant difference (F = 0.26, df = 1 and 28, P = 0.61, power = 0.69).

DISCUSSION

If melanin plays a defensive role against feather lice and other ectoparasites, we might predict that highly melanistic color morphs (e.g. spread pigeons) should have fewer lice than morphs with less melanin (e.g. blue-bar pigeons). We tested this prediction by comparing the abundance of wing and body lice on free-ranging birds of five dissimilar color morphs. Contrary to our prediction, the abundance of lice on spread birds was not lower than that on other color morphs, which suggests that

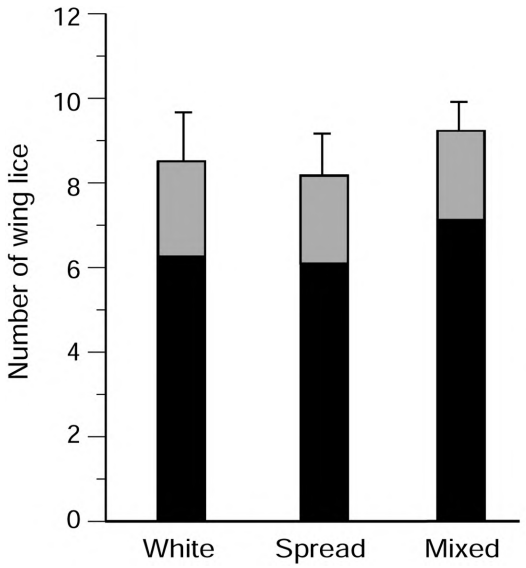

FIG. 3. Experiment II: Survival and reproduction of wing lice in tubes containing white, spread (= black), or mixed feathers (n = 15 tubes per treatment). Bars are the mean (+SE) number of adult (black) and immature (gray) lice at the end of the experiment.

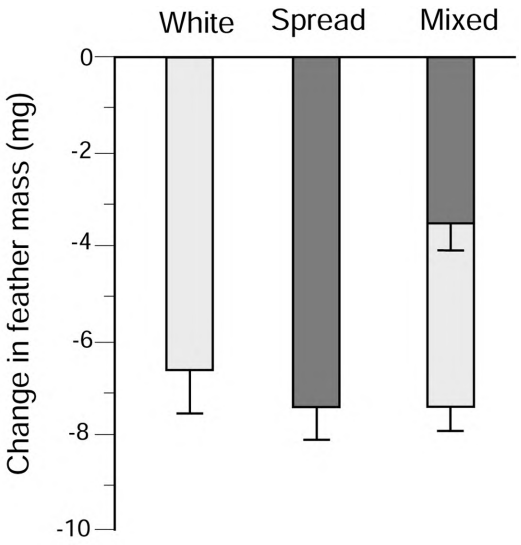

FIG. 4. Experiment II: Mean (–SE) change in mass of feathers from different Rock Pigeon color morphs over the one-month experiment (n = 15 tubes per treatment).

eumelanin does not deter feather-feeding lice. The only significant difference we detected was that the abundance of wing lice on ash birds was lower than that on spread and blue-checker birds (Fig. 1A), which suggests that phaeomelanin may deter lice. However, this result was based on a sample of only five ash birds (albeit from bridges near different towns) and the result was significant only when wing and body lice were analyzed separately. Furthermore, experiment I revealed no difference in the feeding or survival rates of lice on ash feathers as compared with other feathers.

In experiment I, we compared the survival and feeding rates of lice confined to feathers of four color morphs: white, blue-bar, ash, and spread. The results showed no significant difference in survival of wing lice or body lice over the course of the two-week experiment. Furthermore, the feeding rates of lice did not differ significantly among the four color morphs. Feather consumption was confirmed by frass collected from the bottoms of tubes. Furthermore, the frass in a given tube was similar in color to the feathers in that tube, showing that eumelanin and phaeomelanin were being consumed and passed through the digestive system. In short, experiment I provided no support for any effect of phaeomelanin or eumelanin on feather-feeding lice.

If phaeomelanin does not deter lice, why did ash birds have fewer wing lice than the other color morphs (Fig. 1)? The answer may be related to cryptic coloration, which is believed to help lice avoid preening by the host; preening is the principal avian defense against lice and other ectoparasites (Clayton et al. 1999). Some lice species match the color of their host's plumage, which suggests that they have evolved crypsis to avoid visual detection by the preening host (Rothschild and Clay 1952). Ash birds have the lightest-colored flight feathers of any of the color morphs in Figure 1. It is conceivable that pigeon wing lice, which are dark brown, are more visible and therefore more vulnerable to preening on ash birds. Unlike wing lice, body lice were not less abundant on ash birds; why not? This result is also consistent with the crypsis hypothesis, because host vision is presumably less important in the preening of body lice, which are usually buried deep within the downy matrix of abdominal contour feathers. By contrast, wing lice are often quite visible on the two-dimensional undersurface of the wing. The crypsis hypothesis could be tested experimentally by comparing the

effect of preening on wing lice on pigeons of different colors. Data on the louse loads of a larger sample of free-ranging ash-colored pigeons are also needed.

We conducted a second experiment to test possible long-term (four-week) effects of eumelanin on lice. We monitored the survival and reproductive success of wing lice in tubes containing feathers from the two most extreme color morphs, white and spread. We also tested habitat and feeding preferences of lice in mixed tubes containing both kinds of feathers. The results showed no significant difference in survival or reproductive success. Furthermore, lice showed no evidence of habitat or feeding preferences, though the statistical power of these tests was somewhat below the preferred standard of 0.8 (Cohen 1988). Frass collected from tubes with white feathers was white; that from tubes with spread feathers was black; and that from mixed tubes was an assortment of white, black, and gray. When given the option, lice eat and digest both white and dark feathers. Thus, experiment II provided no evidence for any deterrent effect of melanin on Rock Pigeon wing lice.

Our data are inconsistent with the results of Kose et al. (1999), who demonstrated significant habitat preference by Barn Swallow lice for white regions of host tail-feathers in petri dishes. The authors also showed that white spots on the tails of live birds have more holes of the type chewed by Barn Swallow lice (Møller 1991), which suggests a feeding preference for white regions. Unfortunately, the authors did not determine whether lice suffer fitness consequences when eating melanin-rich feathers; such a test was beyond the scope of their study. In the future, experiments are needed to determine whether or not melanin deters Barn Swallow lice. Additional experiments are needed to test whether melanin is a defense against other "ectoparasites," such as feather-degrading bacteria (Burtt and Ichida 1999). Recent *in vitro* evidence suggests that melanin makes feathers more resistant to such bacteria (Goldstein et al. 2004). But tests of the effect of melanin on the bacteria of wild birds, and any resulting effect on host fitness, are still needed.

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